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## Behavioral Response of the Coachwhip (*Masticophis flagellum*) to Habitat Fragment Size and Isolation in an Urban Landscape

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**ABSTRACT.**—Habitat fragmentation is a significant threat to biodiversity worldwide. Habitat loss and the isolation of habitat fragments disrupt biological communities, accelerate the extinction of populations, and often lead to the alteration of behavioral patterns typical of individuals in large, contiguous natural areas. We used radio-telemetry to study the space-use behavior of the Coachwhip, a larger-bodied, wide-ranging snake species threatened by habitat fragmentation, in fragmented and contiguous areas of coastal southern California. We tracked 24 individuals at three sites over two years. Movement patterns of Coachwhips changed in habitat fragments. As area available to the snakes was reduced, individuals faced increased crowding, had smaller home-range sizes, tolerated greater home-range overlap, and showed more concentrated movement activity and convoluted movement pathways. The behavioral response shown by Coachwhips suggests, on a regional level, area-effects alone cannot explain observed extinctions on habitat fragments but, instead, suggests changes in habitat configuration are more likely to explain the decline of this species. Ultimately, if “edge-exposure” is a common cause of decline, then isolated fragments, appropriately buffered to reduce emigration and edge effects, may support viable populations of fragmentation-sensitive species.

Habitat fragmentation occurs when human land use alters continuous, natural landscapes leading to a reduction of total area, changes in patch configuration, and isolation of habitat remnants. Habitat fragmentation threatens the viability of populations (Saunders et al., 1991; Fahrig and Merriam, 1994; Laurance et al., 2002) and worldwide biodiversity (Wilcox and Murphy, 1985; Wilson, 1992). Early interpretations of empirical studies indicated habitat loss has a larger impact on ecological systems than does habitat configuration (Fahrig, 2003; Turner, 2005). However, because habitat loss and configuration covary, the regression-based approaches used in these earlier studies can produce opposing conclusions (Koper et al., 2007).

Species–area relationships strongly suggest that loss of habitat associated with habitat fragmentation will reduce biodiversity independent of the remaining configuration, and studies support these predictions (Lomolino, 1994; Rosenzweig, 2004; Yaacobi, 2007). However, species–area relationships also contain a sliver

of hope where management strategies, such as conserving habitat diversity across remaining patches, allowing movement between patches, improving matrix quality, and reducing edge effects, may allow a system of fragments to conserve more species than would be predicted from the species–area relationship alone (Rosenzweig, 1995, 2003). Doing so requires understanding why species go extinct in fragments and developing methods to decrease this probability.

Larger bodied or wide-ranging species are often key foci of management and conservation goals and also tend to have large space use requirements, making them relatively more susceptible to declines in fragmented landscapes than species using less space. The Coachwhip, *Masticophis flagellum*, is a larger-bodied, wide-ranging snake (Secor and Nagy, 1994; Secor, 1995) that is sensitive to habitat fragmentation (Mitrovich, 2006). Throughout California, the Coachwhip has declined from much of its historic range (Jennings and Hayes, 1994; Case and Fisher, 2001). From 1995 through 2001, a regional (south of Los Angeles, to the U.S.-Mexico Border) reptile-monitoring project sampled 61 locations across a gradient of patch size and isolation (Fisher and Case, 2000; Fisher et al., 2002). Relative to prefragmentation surveys in the same area (Klauber, 1931, 1939),

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the Coachwhip has disappeared from approximately half of the study sites, with isolated fragments (i.e., fragments less than 2,500 ha in size and surrounded by urban development) nine times less likely to maintain populations than sites in nonisolated habitats (Mitrovich, 2006). Given their occurrence on fragments is rare, the persistence of Coachwhips on some isolated fragments in coastal southern California is of interest. These isolated populations seem to be an example of novel habitat management of fragmented landscapes allowing an otherwise sensitive species to "beat the species-area curve." By describing and comparing the space-use behavior of the Coachwhip in these isolated fragments, as well as, in nonfragmented habitats of coastal southern California, we explore the species' behavioral response to changes in fragment size. Comparisons in behavior allow us to evaluate the role of habitat loss versus habitat fragmentation in explaining why wide-ranging species suffer from a greater extinction risk in fragmented landscapes. Lessons learned are applicable to land management strategies aimed at reducing extinction rates of sensitive species in fragmented systems.

Here, we present analyses of radio-telemetry data from 24 individuals of the Baja California Coachwhip, *Masticophis flagellum fuliginosus*, the focal taxon for this study. Individuals were tracked at three sites over two years. We report results related to common space-use parameters (sensu Andreassen et al., 1993) including (1) home-range size; (2) movement patterns within individual home ranges; and (3) extent of home-range overlap among individuals.

#### MATERIALS AND METHODS

**Overview and Study Sites.**—We studied animals at three sites in two geographic areas of coastal southern California. North River and South River sites were located at the Tijuana River National Estuarine Research Reserve (TRNERR) in San Diego County, California (32°34'N, 117°07'W, 0–6 m elevation). This 1,024-ha reserve is isolated by ocean, a military airfield, agriculture, and urban development in San Diego (United States) and Tijuana (Mexico). North River and South River sites were located in upland areas of the estuarine reserve and were isolated from each other by the mouth of the Tijuana River (Fig. 1, no snakes were ever documented crossing the river during seven years of U.S. Geological Survey [USGS] capture recapture-sampling [RNF, unpubl. data], or during radio-tracking). Approximately 50 ha of suitable upland habitat largely surrounded by salt marsh occurred at North River and 150

ha at South River. The third site, Rancho Jamul Ecological Reserve (RJER), was located 28 km east of TRNERR, in San Diego County, California (32°40'N, 116°51'W, 187–381 m elevation). This 1,915-ha reserve was embedded in a larger contiguous natural landscape of sage scrub and grassland, riparian scrub, and fallow agricultural fields (Fig. 2), all habitat types suitable for use by Coachwhips. Coachwhips at this inland reserve exist with virtually unlimited space at the local spatial scale.

We sampled 4–22 trap-lines daily during 12 trapping sessions from April to August in 2002 and 2003. A trap-line consisted of a single shade cloth drift-fence (15 m long, 0.3 m high) with two shaded, hardware cloth box funnel traps (20 × 30 × 50 cm) at either end. To compare prey abundance, and snake communities at the different sites, all small vertebrates captured at the trap-lines were identified, recorded, and released. Trap-lines were haphazardly placed in the best suitable habitat for Coachwhips. Snakes were opportunistically added to the study during the two years; hence, some individuals have longer periods of tracking than others.

**Telemetry.**—We used receivers (models TR-4 and TR-5) and directional antennas (model RA-2AK) from Telonics, Inc., and two types of temperature-sensitive transmitters from Holohil Systems Ltd. Smaller snakes received the SB-2T (5.5 g, 9 × 19 mm), and larger snakes received the SI-2T (9.2 g, 10 × 33 mm). Following Hardy and Greene (1999) transmitter mass as a percentage of animal body mass was kept well below the maximum recommended 5% (range = 1.2–3.3%, Mean ± 1 SE = 2.3 ± 0.1%). Surgical procedures followed the guidelines described by Reinert and Cundall (1982) and Hardy and Greene (1999) and had approval by Animal Use Committee of San Diego State University (protocol 01-018D).

**Field Protocols.**—We determined locations of individuals on average every third day (SE ± 0.2) during the months of greatest activity (March through December). Whether located above or below ground, we recorded GPS coordinates directly above the snake with a handheld unit (Garmin 12-XL, UTM coordinate system, ~4.0 m accuracy). When snakes were located below ground, the location was flagged and considered as a retreat site. Retreat sites were typically small mammal burrows.

**Statistical Analyses.**—We analyzed the movement data for differences in space-use by sex, size, site, and season. We defined the different seasons as spring (20 March through 20 June), summer (21 June through 22 September), and fall (23 September through 20 December), ignoring winter (21 December through 19 March) because movement was so rare. We

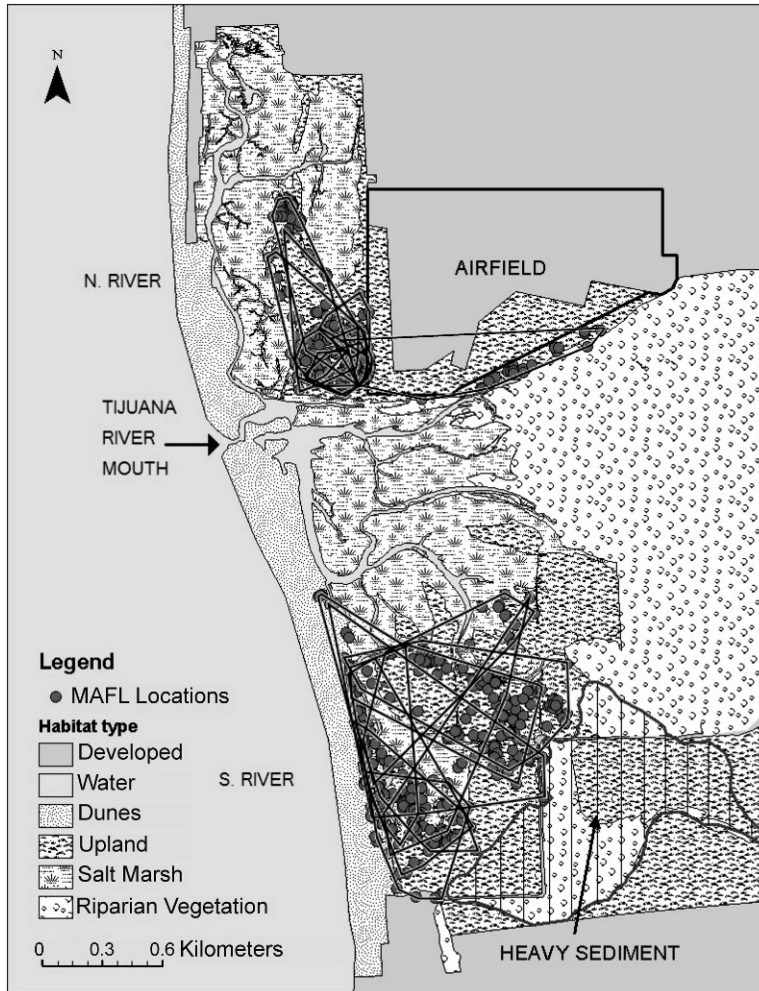


FIG. 1. Configuration of habitat types at the Tijuana River National Estuarine Research Reserve. Points mark all Coachwhip (MAFL) locations for the North River ( $N = 594$ ) and South River ( $N = 561$ ) sites. Individual minimum convex polygon home ranges are shown as overlapping, grey-outlined polygons. No snakes ever crossed the Tijuana River during the course of the study. Upland areas of the airfield were routinely mowed by the U.S. Navy to remove vegetative cover for reasons unrelated to snakes or conservation. Removal of vegetation appears to influence Coachwhip movement. Portions of the South River study area are covered by substantial sediment and debris flows which also appear to influence Coachwhip movement (hatched polygon reflects area influenced by debris flows). Upland areas in the reserve consisted largely of sage scrub and grassland, dune vegetation, and wetland-upland transition zone species, such as California box-thorn (*Lycium californicum*) and California salt bush (*Atriplex californica*).

combined trap-line capture data across years and analyzed the data for differences in capture rates of small mammals, lizards, and snakes across sites.

We used the Animal Movement extension (Hooge and Eichenlaub, 1997) in ArcView 3.3 to estimate home-range size. We calculated home-range size as 100% minimum convex polygon (MCP) and fixed 95% kernel home range (KHR). For KHR calculations, we used least-squares cross-validation to determine the smoothing

factor (Seaman and Powell, 1996; Blundell et al., 2001). For the home-range overlap analyses, we considered the proportion of an individual's MCP home range shared by other individuals as overlap.

We estimated three distinct components of movement: (1) distance of movements; (2) frequency of movement; and (3) the fractal dimension or tortuosity of the movement path (Dicke and Burrough, 1988). To calculate the distance of movements, we first measured the



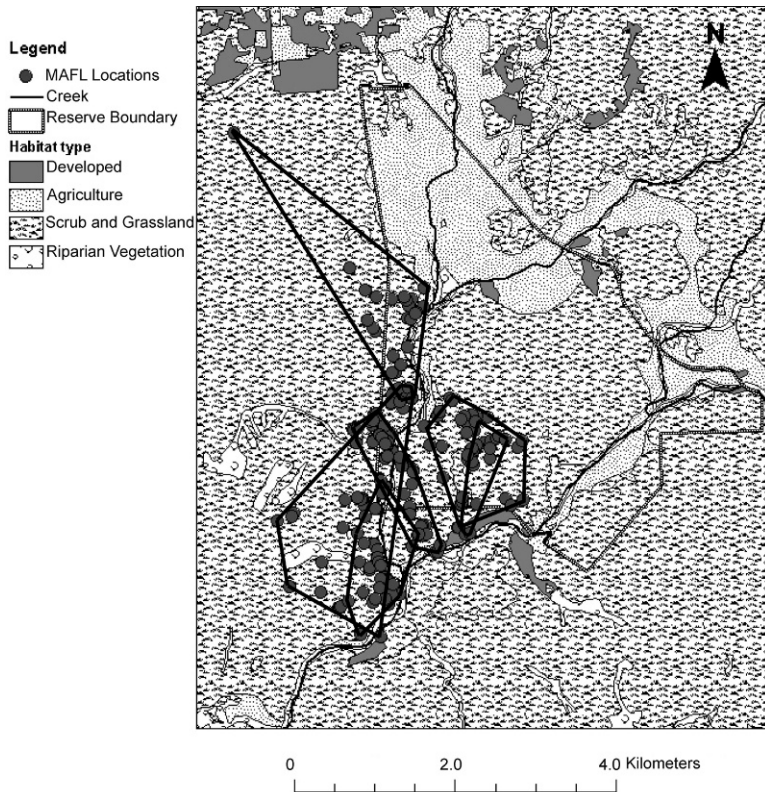


FIG. 2. Configuration of habitat types and Coachwhip (MAFL) locations (points;  $N = 324$ ) at the Rancho Jamul Ecological Reserve (RJER) site. Minimum convex polygon home ranges (solid black-outlined polygons) show patterns of overlap and differences in home-range size between individuals. Average home-range size at RJER is 4 and 12 times greater than average home-range sizes at South River and North River, respectively. Sage scrub and grassland habitats dominated the site. Agricultural fields were fallow and largely dominated by introduced, annual grasses. Topographical variation (not shown) is much greater at RJER than South River and North River sites.

mean distance traveled per day to estimate an overall rate of movement. Distance traveled per day, recommended by Gregory et al. (1987), was measured across a sequential pairs of fixes (the distance traveled between two fixes divided by the number of days between the two fixes) producing a distribution of distances (Difffendorfer et al., 2005). Mean distance of movements (i.e., mean distance traveled per move) was identical to the mean distance traveled per day, except movements of zero were excluded. Because the accuracy of our GPS unit was  $\sim 4.0$  m, we defined movements as a sequential pair of fixes resulting in a net displacement of 8 m or more. We estimated the frequency of movement by calculating the proportion of fixes resulting in moves for each individual. We used the program Fractal 4.0 (Nams, 1996) to calculate the fractal dimension of the movement path. This measurement is a scale-independent estimate of movement path tortuosity, or

crookedness that varies from one to two (Weins et al., 1995). A value of one indicates the path is straight and a maximum value of two indicates the path is so convoluted as to completely cover a plane.

To avoid pseudoreplication, we used individuals as replicates in our statistical tests. We tested for differences in sampling effort by comparing the duration of tracking (number of days between the release date and final date monitored) and the number of fixes per individual between sites using one-way ANOVAs. We checked for differences in the mean number of days between successive locations by site using a one-way ANOVA. We used two-way ANOVAs to check for differences in body mass and size between sexes within and across sites. We used a correlation to test for a relationship between number of locations and home-range size.

We compared estimates of home-range size, fractal dimension of the movement path, and

home-range overlap by the main effects of site, sex, and body size, and site  $\times$  sex, and site  $\times$  body size interactions using GLMs (SYSTAT 11.0, SYSTAT Software, Inc.). Distances moved were averaged across all individuals (i.e., we computed a mean for each individual and got 1 df for that individual) and, along with the frequency of movement, compared across seasons using one-way ANOVAs. We then used GLMs to check for differences in distances moved and frequency of movement between site, sex, and body size, and site  $\times$  sex, and site  $\times$  body size for each season separately.

We combined all the movements of individuals for each site and used Kolmogorov-Smirnov (K-S test) and Pearson chi-square tests to check for differences in the distribution of movement distances between sites. Finally, we used the Kruskal-Wallis test to check for differences in lizard and small mammal density, Coachwhip, and snake capture rates among sites. Because small mammal, lizard, and snake species (other than the Coachwhip) were not marked, and Coachwhip recaptures too few in number to produce reliable estimates of abundance using recapture data (White et al., 1982), we realized it would be necessary to use capture data as our indices of abundance even though these could be biased by capture probability (Nichols, 1992). Means are given  $\pm$  1 SE.

## RESULTS

We obtained movement data from 24 (14 male and 10 female) Coachwhips. Nine were located at North River, 9 at South River, and 6 at RJER. Snout-vent length (SVL) ranged from 0.86–1.32 m ( $1.04 \pm 0.02$  m,  $N = 24$ ) and body mass from 180–665 g ( $373 \pm 29$  g,  $N = 24$ ). We found no difference between sexes within or among sites in SVL (sex  $F_{1,18} = 0.821$ ,  $P > 0.05$ ; site  $F_{2,18} = 0.044$ ,  $P > 0.05$ ; sex  $\times$  site  $F_{2,18} = 0.075$ ,  $P > 0.05$ ) or mass (sex  $F_{1,18} = 1.785$ ,  $P > 0.05$ ; site  $F_{2,18} = 0.235$ ,  $P > 0.05$ ; sex  $\times$  site  $F_{2,18} = 0.060$ ,  $P > 0.05$ ). We recorded 1,479 total locations of radio-tagged snakes during the two-year study. Although the number of locations varied among individuals, seasonal variability in sampling effort between sites and sexes was minimal (Table 1). The duration of tracking and number of fixes per snake did not differ across sites. We found no correlation between home-range size and number of fixes. Uneven terrain at RJER and the propensity of snakes to shift centers of activity resulted in more days between successive fixes at RJER than South River and North River ( $F_{2,21} = 8.4$ ,  $P < 0.005$ , RJER:  $4.2 \pm 0.3$  days,  $N = 6$ , South River:  $2.6 \pm 0.24$  days,  $N = 9$ , North River:  $2.6 \pm 0.33$  days,  $N = 9$ ).

TABLE 1. Total number of fixes by site, season, and sex. Total number of radio-tracked Coachwhips making up the fixes is in the parentheses. For all sites, fixes were obtained in 2002 and 2003.

Season	Sex	Study site		
		North River	South River	RJER
Spring	Male	46 (4)	75 (4)	51 (3)
	Female	24 (2)	68 (3)	67 (3)
Summer	Male	235 (6)	178 (4)	61 (3)
	Female	135 (3)	132 (4)	94 (3)
Fall	Male	94 (6)	71 (4)	12 (3)
	Female	50 (3)	24 (2)	31 (3)
Total number of snakes		9	9	6

**Home-Range Size.**—The minimum convex polygon (MCP) and 95% kernel home-range (KHR) methods produced similar estimates of home-range size with both estimates varying similarly among individuals and sites. We found differences in MCP area across sites, between snakes of different body sizes, and an interaction effect of body size and site (site  $F_{2,18} = 21.027$ ,  $P < 0.0001$ ; SVL  $F_{1,18} = 21.117$ ,  $P < 0.0001$ ; site  $\times$  SVL  $F_{2,18} = 17.136$ ,  $P < 0.0001$ ). Snakes at RJER maintained home ranges 4 times greater, on average, than home ranges of snakes from South River and 12 times greater than home ranges of snakes from North River (RJER:  $136.4 \pm 36.83$  ha,  $N = 6$ , South River:  $33.7 \pm 4.26$  ha,  $N = 9$ , North River:  $11.18 \pm 3.05$  ha,  $N = 9$ ). In general, home range decreased with increases in body size. For example, at RJER smaller bodied snakes maintained the largest home ranges. However, at North River, larger bodied snakes maintained the largest home ranges (Fig. 3; RJER  $r_7 = -0.83$ ,  $P < 0.05$ ; North River  $r_4 = 0.69$ ,  $P < 0.05$ ). Collectively, snakes tracked at RJER occupied a total area of approximately 1,500 ha, an area 10 and 30 times greater in size than the total area available to South River and North River individuals, respectively.

**Distances Moved.**—Frequent short distance movements with increasingly rarer longer distance movements resulted in right-skewed distributions of distances moved per day for all individuals across all sites (Table 2). The frequency distributions of distances moved varied among sites (K-S test: North River vs. South River,  $P < 0.0001$ ; North River vs. RJER,  $P < 0.05$ ; South River vs. RJER  $P < 0.05$ ), with a higher frequency of shorter distance movements ( $< 100$  m) distinguishing North River movements from South River and RJER (Table 2;  $\chi^2_{6,934} = 28.3$ ,  $P < 0.0001$ ).

The average daily movements by individuals varied widely across seasons ( $F_{2,55} = 36.251$ ,  $P$

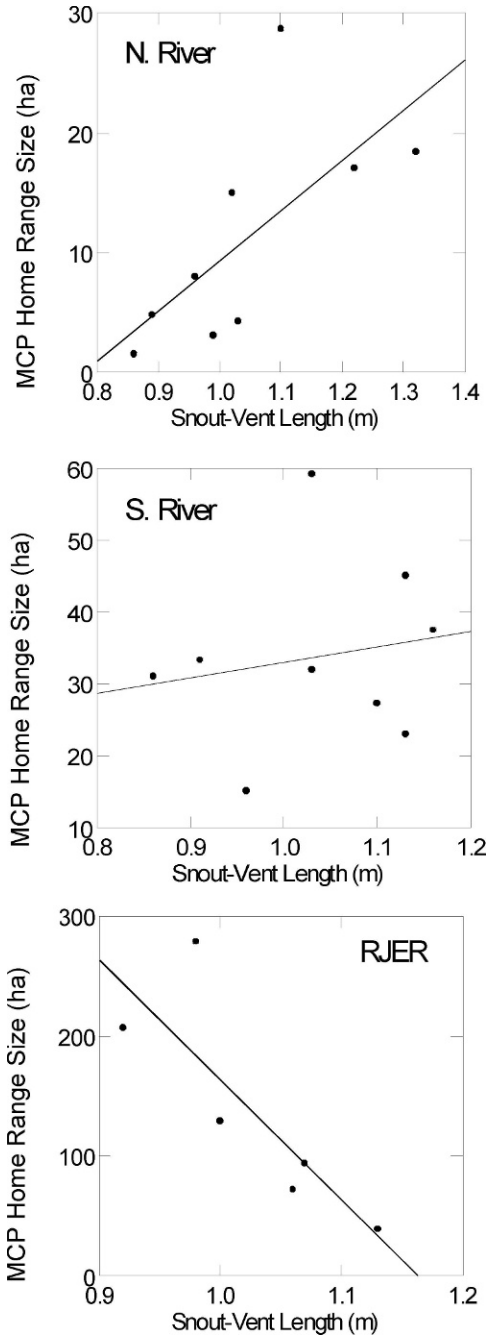


FIG. 3. Scatter-plots of minimum convex polygon (MCP) home-range size versus body size (snout-vent length) for the three sampled sites (North River:  $N = 9$ , South River:  $N = 9$ , and RJER:  $N = 6$ ). The relationship of home-range size to body size is reversed between North River and RJER sites.

TABLE 2. Number of movements (% of total) for all Coachwhips combined by site and distributed by movement category. Movements or distances moved were measured in meters per day.

Movement category	North River	South River	RJER
0–100 m	270 (81)	234 (64)	165 (70)
101–200 m	45 (14)	82 (23)	50 (21)
201–300 m	11 (3)	26 (7)	9 (4)
> 300 m	7 (2)	23 (6)	11 (5)

< 0.0001) with peaks in spring, followed by summer, and lowest values in fall (spring:  $136 \pm 17$  m/day,  $N = 17$ , summer:  $65 \pm 4.7$  m/day,  $N = 23$ , fall:  $20 \pm 3.2$  m/day,  $N = 19$ ). Eighty-nine percent of the farthest 5% of the distances moved (range: 281–1,004 m/day,  $389 \pm 20$  m/day,  $N = 47$ ) occurred in spring. We found differences in the length of movements in spring between sexes (sex  $F_{1,15} = 5.331$ ,  $P < 0.05$ ) with males moving substantially longer distances than females (Males:  $165 \pm 23$  m/day,  $N = 10$ , Females:  $94 \pm 15$  m/day,  $N = 7$ ).

Summer movements varied between site, sex, and an interaction effect of site and SVL (site  $F_{2,17} = 10.523$ ,  $P < 0.001$ ; sex  $F_{1,17} = 9.616$ ,  $P < 0.01$ ; site  $\times$  SVL  $F_{2,17} = 9.214$ ,  $P < 0.005$ ). Snakes from North River moved shorter average distances than snakes from South River and RJER (RJER:  $72 \pm 11$  m/day,  $N = 6$ , South River:  $71 \pm 6.3$  m/day,  $N = 8$ , North River:  $56 \pm 7.5$  m/day,  $N = 9$ ), and males outdistanced females (Males:  $73 \pm 5.4$ ,  $N = 13$ , Females:  $56 \pm 7.4$ ,  $N = 10$ ). At North River, larger bodied snakes moved further distances than smaller bodied snakes (North River  $r_7 = 0.80$ ,  $P < 0.01$ ), whereas at South River and RJER, body size was not related to distances moved.

In the fall, when distances moved for all snakes declined sharply, we found a difference in distances moved between sites and an interaction between site and sex (site  $F_{2,13} = 4.381$ ,  $P < 0.05$ ; site  $\times$  sex  $F_{2,13} = 3.851$ ,  $P < 0.05$ ). Snakes at RJER moved the shortest average distances of the three sites (RJER:  $8.6 \pm 1.7$  m/day,  $N = 5$ , South River:  $28 \pm 8.0$  m/day,  $N = 5$ , North River:  $22 \pm 3.7$  m/day,  $N = 9$ ). Males from South River dramatically outdistanced females, whereas differences between the sexes were minimal at the other two sites (RJER males:  $7.0 \pm 2.0$  m/day,  $N = 2$ , RJER females:  $9.7 \pm 2.7$  m/day,  $N = 3$ , South River males:  $40.7 \pm 5.5$  m/day,  $N = 3$ , South River females:  $11.0 \pm 5.0$  m/day,  $N = 2$ , North River males:  $24 \pm 5.1$  m/day,  $N = 6$ , North River females:  $20 \pm 5.5$  m/day,  $N = 3$ ).

*Frequency of Movement.*—The chance an individual moved was greatest during the spring

TABLE 3. Sampling effort, defined as the number of nights sampled and mean ( $\pm$  SE) number of traps sampled per night, and mean ( $\pm$  SE) capture rate per 80 trap-nights for Coachwhips, snakes other than Coachwhips, small mammals (i.e., mice of the Heteromyidae and Muridae families), and lizards by site, summed across 2002 and 2003 field seasons.

Site	Nights sampled	Traps sampled	Coachwhips	Snakes other than Coachwhips	Small mammals	Lizards
North River	42	16.0 $\pm$ 0.0	1.8 $\pm$ 0.5	2.4 $\pm$ 0.6	10.4 $\pm$ 1.4	5.6 $\pm$ 1.2
South River	36	61.3 $\pm$ 2.4	0.6 $\pm$ 0.1	0.6 $\pm$ 0.1	12.3 $\pm$ 0.9	6.2 $\pm$ 1.2
RJER	44	63.4 $\pm$ 1.5	0.2 $\pm$ 0.1	3.8 $\pm$ 0.5	12.6 $\pm$ 0.8	4.7 $\pm$ 0.5

and summer, dropping sharply in the fall ( $F_{2,55} = 24.102$ ,  $P < 0.001$ , spring:  $0.76 \pm 0.03$ ,  $N = 17$ , summer:  $0.75 \pm 0.03$ ,  $N = 23$ , fall:  $0.46 \pm 0.05$ ,  $N = 18$ ). In spring, snakes at RJER moved more frequently than did snakes from the South River and North River sites (RJER:  $0.83 \pm 0.04$ ,  $N = 6$ , South River:  $0.77 \pm 0.04$ ,  $N = 5$ , North River:  $0.69 \pm 0.07$ ,  $N = 6$ , site  $F_{2,11} = 4.84$ ,  $P < 0.05$ ). In the summer and the fall, proportional movement was similar across sites, sexes, and body size.

**Movement Path Tortuosity.**—We found differences in the fractal dimension, or structure of the movement path between sites, sex, and an interaction between site and sex (site  $F_{2,18} = 24.979$ ,  $P < 0.0001$ ; sex  $F_{1,18} = 6.905$ ,  $P < 0.05$ ; and site  $\times$  sex  $F_{2,18} = 4.964$ ,  $P < 0.05$ ). Snakes from North River generated a more convoluted movement path ( $1.39 \pm 0.03$ ,  $N = 9$ ) than snakes from South River ( $1.26 \pm 0.01$ ,  $N = 9$ ) or RJER ( $1.23 \pm 0.03$ ,  $N = 6$ ). In addition, females at North River ( $1.49 \pm 0.05$ ,  $N = 3$ ) had more convoluted paths than males ( $1.33 \pm 0.02$ ,  $N = 6$ ), but sexes did not differ in movement paths at the other sites.

**Home-Range Overlap.**—We found the extent of home-range overlap varied by site and an interaction effect of site  $\times$  SVL (site  $F_{2,18} = 7.523$ ,  $P < 0.005$ ; site  $\times$  SVL  $F_{2,18} = 6.705$ ,  $P < 0.01$ ). Snakes from South River had 40% ( $0.89 \pm 0.03$ ,  $N = 9$ ) and snakes from North River 32% ( $0.81 \pm 0.1$ ,  $N = 9$ ) greater overlap than snakes from RJER ( $0.49 \pm 0.14$ ,  $N = 6$ ). Home-range overlap was much greater for larger bodied snakes relative to smaller bodied snakes at RJER ( $r_4 = 0.96$ ,  $P < 0.005$ ) while equivalent across SVL for South River and North River.

**Prey and Snake Capture Rates.**—In 2002 and 2003, we trapped 5,670 trap-nights across the three sites. Capture rates for Coachwhips increased with decreasing fragment size (Table 3; Kruskal-Wallis test:  $\chi^2_{2,121} = 6.382$ ,  $P < 0.05$ ). At North River, we captured Coachwhips 10 times more frequently than at RJER and at South River 3 times more frequently than at RJER. Small mammals and lizards had similar

abundances and community composition among sites (Table 3). We found no difference in lizard (Kruskal-Wallis test:  $\chi^2_{2,121} = 1.945$ ,  $P > 0.05$ ) capture rates and a slight decrease in small mammal capture rates at North River ( $\chi^2_{2,121} = 6.263$ ,  $P < 0.05$ ). The snake community varied little in composition among North River and South River (same three snake species at both sites) but substantially between the two TRNERR sites and RJER (nine snake species present at RJER; MJM, unpubl. data). Finally, capture rates of snake species other than the Coachwhip were greatest at RJER, followed by North River, and then South River (Table 2;  $\chi^2_{2,121} = 26.059$ ,  $P < 0.001$ ).

## DISCUSSION

Our data reveal evidence of great plasticity in the space-use behavior of Coachwhips in fragmented habitats. Collectively, results from all three sites suggest Coachwhips adjusted their space-use behavior in a stepwise manner to changes in fragment size. As habitat fragments decreased in size and increased in isolation, snakes tolerated more crowded conditions, reduced home-range size, and increased home-range overlap. The smaller home ranges and increased overlap are consistent with expectations for nonterritorial animals exhibiting a fusion response to habitat fragmentation (Ims et al., 1993; Andreassen et al., 1998). This response, also termed a crowding effect by Lovejoy et al. (1986), predicts snakes in smaller fragments will tolerate less space and greater overlap as intraspecific competition for resources intensifies with a decrease in fragment size.

Snakes in the large contiguous natural landscape at RJER maintained home-range sizes and movement patterns similar to other free-ranging, unbounded populations of Coachwhips. Here, snakes maintained home ranges among the largest ever reported for snake species (Macartney et al., 1988) while consistently shifting their centers of activity throughout the field season. This wide-ranging space-use has



been reported across most of the Coachwhip's geographic range: southern California (U.S.), the Mojave Desert (Secor and Nagy, 1994; Secor, 1995), eastern Texas (M. Keck, pers. comm.), and north-central Florida (Dodd and Barichivich, 2007). This consistency in space-use among populations from different geographic regions suggests widely foraging behavior is a common feature of Coachwhip biology and possibly reflects an ancestral condition resulting from strong selective pressure for efficient exploitation of patchy, ephemeral resources characteristic of the desert environment where this species first evolved (Ortenburger, 1928; Wilson, 1970).

At South River, the larger of the two habitat fragments, snakes tolerated an estimated tripling in density, a fourfold reduction in average home-range size and 40% greater home-range overlap relative to RJER. With the amount of useable habitat at South River approximately one-tenth the total area used by snakes at RJER, the fragment was large enough for "everyday" movement patterns to not be affected, yet too small to allow longer distance, exploratory movement. We found no real difference between South River and RJER populations in the common space-use parameters reflecting most daily movement processes. Average length of movements was similar during the seasons of greatest activity (i.e., spring and summer). Difference in proportional movement was minimal and structure of the movement pathway (i.e., directionality of movement) was equivalent. Even though they occupied a much smaller habitat fragment the snakes still exhibited the basic components of Coachwhip movement behavior prevalent in nonfragmented systems. The large difference in home range between sites was caused by an absence of longer distance movement by the snakes at South River. Longer distance, exploratory movement was likely limited as a result of the smaller size of the South River site. Multiple times during the tracking season individuals moved to the edge of the reserve only to return (unpubl. data). These were likely attempts at long distance movements that were aborted and resulted in the snakes reusing areas of the home range more intensively than RJER.

At North River, the smaller fragment, with a total amount of useable habitat approximately one-thirtieth the total area used by snakes at RJER, all space-use behaviors were disrupted relative to the other sites as snakes concentrated their activity in a much reduced space. Here, snakes tolerated an estimated 10-fold increase in density, 12-fold reduction in home-range size, and a 32% greater home-range overlap relative to RJER. The consequence of the altered

movement patterns was a substantial reduction in overall movement rate and increase in the intensity of use of the areas within the home range. Relative to RJER and South River, snakes at North River moved less often during the spring and summer and traveled shorter distances in the summer. Likely reflecting the severe spatial limitations of the site and conditions of increased crowding, snakes at North River generated a more convoluted movement pathway relative to individuals at the larger South River and RJER.

Interestingly, at North River, larger snakes had larger home-range sizes, whereas at RJER smaller snakes had larger home ranges. It appears that determinants of size-specific movement operating in these two systems are different. At the North River site, it is possible that with increased crowding there is strong selection to minimize exploratory movement and maximize local foraging activity and thus efficiency. Snakes searching for prey in areas recently used by conspecifics may experience lower foraging success (Webb and Shine, 1997). At high densities, prey availability may be low everywhere; thus, conserving energy by moving less may be an effective strategy. In addition, cannibalism has been observed in Coachwhips and might explain less movement in smaller snakes as they attempt to avoid larger animals actively searching for prey (Matos, 2004). At RJER the difference in home-range size between larger and smaller bodied snakes appears to result from smaller snakes moving greater distances in the summer. We found no difference in the frequency or directionality of movement, or distance of movement in the spring and fall between snakes of different body sizes. Because most reproductive activity had ceased by the end of the spring season (pers. obs.), we attribute this difference in the summer to a difference in foraging behavior as younger snakes search for novel food resources to exploit.

Differences in prey abundances across the sites did not cause the changes in space use. The capture rates and community composition of small mammals and lizards, the principal prey of Coachwhips, showed little variation among sites. The differences in snake communities and abundances between RJER and the North and South River sites could depress the availability of food resources through competition and, thus, account for some of the behavioral differences between RJER and the two TRNERR sites. However, increased competition cannot account for the observed differences in behavior between North River and South River sites, as North River maintained a greater density of snakes. Furthermore, the close proximity (<2 km) of the North River and South River sites to each other suggests other external

factors (e.g., predators and other competitors) would be similar and not account for the observed differences in behavior. Instead, the single consistent and greatest difference between sites is their size, and substantial departures in space use behaviors are the results of conditions of limited space present at these two isolated sites.

The great plasticity we observed in space-use behavior suggests Coachwhip snakes might be resistant to the impacts of habitat fragmentation. Unfortunately, this is not the case. Coachwhip populations are disappearing from fragmented landscapes throughout coastal southern California and appear especially vulnerable to the isolating effects of habitat fragmentation (Case and Fisher, 2001; Mitrovich, 2006). Thus, why are Coachwhip populations vulnerable? We recognize two contrasting hypotheses that explain why wide-ranging species suffer from a greater extinction risk in fragmented habitats. The first hypothesis (fixed-area hypothesis) states that wide-ranging species decline in fragmented landscapes because they have large and relatively inflexible individual area requirements (Vos et al., 2001; Henle et al., 2004). The second (edge exposure hypothesis) states wide-ranging species, irrespective of population size, are susceptible to the effects of habitat fragmentation because their movement patterns leave them most exposed to edge effects (Woodroffe and Ginsburg, 1998). Our results show Coachwhips do not have strict individual area requirements. Thus, the "area effect" hypothesis does not explain this species' extinction from fragmented landscapes. Instead, the edge exposure hypothesis better explains the patterns of regional Coachwhip population extinctions. Like large carnivores, snakes in fragmented habitats are exposed to numerous mortality agents outside reserves. These include, common carnivores (e.g., coyotes, skunks, foxes, feral cats, and hawks) associated with urbanization (Crooks, 2000; Unitt, 2004), humans (Klauber, 1972), and human activities, especially vehicular traffic on roads (Seigel, 1986; Dodd et al., 1989; Bernardino and Dalrymple 1992; Rosen and Lowe 1994). As space-use behavior mediates the frequency of contact with humans and edge-adapted predators, edge effects are likely severe for wide-ranging snake species.

Analysis of USGS monitoring data corroborates this hypothesis. In a landscape-scale study conducted in southern California, site occupancy of the Coachwhip was strongly correlated with reduced levels of urban edge while unrelated to the size of the sampled natural area (Mitrovich, 2006). This susceptibility to urban edge is consistent with the patterns reflected in other vertebrates studied in south-

ern California (Case and Fisher, 2001; Laakkonen et al., 2001). In the present study, it is the absence of urban edge that appears to partly explain the ability of the snake populations to persist on the small fragments. The surrounding habitats and land-use practices appear to effectively buffer or insularize Coachwhip populations from edge-effects. At the North River, radio-tracked snakes rarely used the surrounding subtidal salt marsh and manicured grounds of the naval airfield. Similarly, at the South River, the surrounding salt marsh, exposed beaches, dense riparian habitat, and areas adversely affected by sedimentation from tributaries of the Tijuana River (Fig. 1) effectively buffered the snakes from regular contact with urban areas.

Our research suggests Coachwhip declines in southern California are not explained solely by patch size and represent an exception to the hypothesis that negative responses to habitat fragmentation are driven largely by habitat loss. The incredibly high level of space-use plasticity allows high densities of snakes to persist on patches smaller than even a typical home range in continuous habitat. For this species, we must recognize and further investigate the role of habitat configuration and, specifically, edge effects on the viability of populations in reserves surrounded by urban areas. Dodd and Barichivich (2007) indicate large snakes require large amounts of habitat for effective conservation based primarily on their findings of large home ranges. We agree entirely with their proposition, but note that larger areas reduce perimeter to edge ratios and may reduce exposure rates to hostile edges or matrix habitat. In addition, and in agreement with Rosenzweig (2003), our work indicates smaller patches of habitat, if appropriately buffered to reduce emigration and edge effects, may support viable populations of large snakes. Ultimately, if most large-bodied species show space-use plasticity and "edge-exposure" is a common cause of decline, then limiting contact with human activity and edge-adapted predators will likely reduce extinction rates in fragmented systems. In these cases, the combination of maximizing reserve size and minimizing edge effects may allow for continued persistence.

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## LITERATURE CITED

- ANDREASSEN, H. P., R. A. IMS, N. C. STENSETH, AND N. G. YOCOZ. 1993. Investigating space use by means of radio-telemetry and other methods: a methodological guide. In N. C. Stenseth and R. A. Ims (eds.), *The Biology of Lemmings*, pp. 589–618. Academic Press, London.
- ANDREASSEN, H. P., K. HERTZBERG, AND R. A. IMS. 1998. Space-use responses to habitat fragmentation and connectivity in the root vole *Microtus oeconomus*. *Ecology* 79:1223–1235.
- BERNARDINO, F. S., AND G. H. DALRYMPLE. 1992. Seasonal activity and road mortality of the snakes of the Pahay-okee wetlands of Everglades National Park, USA. *Biological Conservation* 62:71–75.
- BLUNDELL, G. M., J. A. K. MAIER, AND E. M. DEBEVEC. 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecological Monographs* 71:469–489.
- CASE, T. J., AND R. N. FISHER. 2001. Measuring and predicting species presence: coastal sage scrub case study. In C. T. Hunsaker, M. F. Goodchild, M. A. Friedl, and T. J. Case (eds.), *Spatial Uncertainty in Ecology*, pp. 47–71. Springer-Verlag, New York.
- CROOKS, K. R. 2000. Mammalian carnivores as target species for conservation in southern California. In J. E. Keeley, M. Baer-Keeley, and C. J. Fotheringham (eds.), *2nd Interface between Ecology and Land Development in California*, pp. 105–112. U.S. Geological Survey Open-File Report 00-62, Sacramento, CA.
- DICKE, M., AND P. A. BURROUGH. 1988. Using fractal dimensions for characterizing tortuosity of animal trails. *Physiological Entomology* 13:393–398.
- DIFFENDORFER, J. E., C. ROCHESTER, R. N. FISHER, AND T. K. BROWN. 2005. Movement and space use by Rosy Boas (*Charina trivirgata roseofusca*) in coastal southern California. *Journal of Herpetology* 39:24–36.
- DODD, C. K., JR., AND W. J. BARICHIVICH. 2007. Movements of large snakes (*Drymarchon*, *Masticophis*) in north-central Florida. *Florida Scientist* 70:83–94.
- DODD, C. K., JR., K. M. ENGE, AND J. N. STUART. 1989. Reptiles on highways in north-central Alabama, USA. *Journal of Herpetology* 23:197–200.
- FAHRIG, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34:487–515.
- FAHRIG, L., AND G. MERRIAM. 1994. Conservation of fragmented populations. *Conservation Biology* 8:50–59.
- FISHER, R. N., AND T. J. CASE. 2000. Distribution of the herpetofauna of coastal southern California with reference to elevation effects. In J. E. Keeley, M. Baer-Keeley, and C. J. Fotheringham (eds.), *2nd Interface between Ecology and Land Development in California*, pp. 137–143. U.S. Geological Survey Open-File Report 00-62, Sacramento, CA.
- FISHER, R. N., A. V. SUAREZ, AND T. J. CASE. 2002. Spatial patterns in the abundance of the coastal horned lizard. *Conservation Biology* 16:205–215.
- GREGORY, P. T., J. M. MACARTNEY, AND K. W. LARSEN. 1987. Spatial patterns and movements. In R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*, pp. 366–395. Macmillan, New York.
- HARDY, D. L., AND H. W. GREENE. 1999. Surgery on rattlesnakes in the field for implantation of transmitters. *Sonoran Herpetologist* 12:26–28.
- HENLE, K., K. F. DAVIES, M. KLEYER, C. MARGULES, AND J. SETTELE. 2004. Predictors of species sensitivity to fragmentation. *Biodiversity Conservation* 13:207–251.
- HOOGE, P. N., AND B. EICHENLAUB. 1997. Animal movement extension to ArcView, Version 2.0. Alaska Biological Science Center, U.S. Geological Survey, Anchorage.
- IMS, R. A., J. ROLSTAD, AND P. WEGGE. 1993. Predicting space use responses to habitat fragmentation: can voles *Microtus oeconomus* serve as an experimental model system (EMS) for Capercaillie Grouse *Tetrao urogallus* in boreal forest? *Biological Conservation* 63:261–268.
- JENNINGS, M. R., AND M. P. HAYES. 1994. Amphibian and reptile species of special concern in California. Final Report to Inland Fisheries Division, California Department of Fish and Game, Rancho Cordova.
- KLAUBER, L. M. 1931. A statistical survey of the snakes of the southern border of California. *Bulletins of the Zoological Society of San Diego* 8:1–93.
- . 1939. Studies of reptile life in the arid southwest. *Bulletins of the Zoological Society of San Diego* 14:1–100.
- . 1972. *Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind*, 2nd ed. University of California Press, Berkeley.
- KOPER, N., F. K. A. SCHMIEGLOW, AND E. H. MERRILL. 2007. Residuals cannot distinguish between ecological effects of habitat amount and habitat fragmentation: implications for the debate. *Landscape Ecology* 22:811–820.
- LAAKKONEN, J., R. N. FISHER, AND T. J. CASE. 2001. Effect of land cover, habitat fragmentation, and ant colonies on the distribution and abundance of shrews in southern California. *Journal of Animal Ecology* 70:776–788.
- LAURANCE, W. F., T. E. LOVEJOY, H. L. VASCONCELOS, E. M. BRUNA, R. K. DIDHAM, P. C. STOUFFER, C. GASCON, R. O. BIERREGAARD, S. G. LAURANCE, AND E. SAMPAIO. 2002. Ecosystem decay of Amazonian Forest fragments: a 22-year investigation. *Conservation Biology* 16:605–618.
- LOMOLINO, M. V. 1994. An evaluation of alternative strategies for building networks of nature reserves. *Biological Conservation* 69:243–249.

- LOVEJOY, T. E., R. O. BIERREGAARD, A. B. RYLANDS JR., C. E. MALCOLM, L. H. QUINTELA, K. S. HARPER, K. S. BROWN JR., A. H. POWELL, G. V. N. POWELL, H. O. R. SCHUBART, AND M. B. HAYS. 1986. Edge and other effects of isolation on Amazon forest fragments. In M. E. Soule (ed.), *Conservation Biology: The Science of Scarcity and Diversity*, pp. 257–285. Sinauer, Sunderland, MA.
- MACARTNEY, J. M., P. T. GREGORY, AND K. W. LARSEN. 1988. A tabular survey of data on movements and home ranges of snakes. *Journal of Herpetology* 22:61–73.
- MATOS, J. A. 2004. *Masticophis flagellum ruddocki*. Cannibalism. *Herpetological Review* 35:401–402.
- MITROVICH, M. J. 2006. A Case Study in Conservation Science: The Spatial Ecology and Evolutionary History of the Coachwhip Snake (*Masticophis flagellum*) and Striped Racer (*M. lateralis*). Unpubl. Ph.D. diss., University of California, Davis, and San Diego State University, San Diego.
- NAMS, V. O. 1996. The VFractal: a new estimator for fractal dimension of animal movement paths. *Landscape Ecology* 11:289–297.
- NICHOLS, J. D. 1992. Capture-recapture methods. *Bioscience* 42:94–102.
- ORTENBURGER, A. I. 1928. The Whip Snakes and Racers: Genera *Masticophis* and *Coluber*. University of Michigan, Ann Arbor.
- REINERT, H. K., AND D. CUNDALL. 1982. An improved surgical implantation method for radio-tracking snakes. *Copeia* 3:702–705.
- ROSEN, P. C., AND C. H. LOWE. 1994. Highway mortality of snakes in the Sonoran Desert of southern Arizona. *Biological Conservation* 68:143–148.
- ROSENZWEIG, M. L. 1995. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- . 2003. Win-Win Ecology: How the Earth's Species Can Survive in the Midst of Human Enterprise. Oxford University Press, New York.
- . 2004. Applying species-area relationships to the conservation of species diversity. In M. V. Lomolino and L. R. Heaney (eds.), *Frontiers of Biogeography: New Directions in the Geography of Nature*, pp. 325–343. Sinauer, Sunderland, MA.
- SAUNDERS, D. A., R. J. HOBBS, AND C. R. MARGULES. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5:18–32.
- SEAMAN, D. E., AND R. A. POWELL. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075–2085.
- SECOR, S. 1995. Ecological aspects of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. *Herpetological Monographs* 9:169–186.
- SECOR, S. M., AND K. A. NAGY. 1994. Bioenergetic correlates of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. *Ecology* 75:1600–1614.
- SEIGEL, R. A. 1986. Ecology and conservation of an endangered rattlesnake, *Sistrurus catenatus*, in Missouri, USA. *Biological Conservation* 35:333–346.
- TURNER, M. G. 2005. Landscape ecology: what is the state of the science? *Annual Review of Ecology, Evolution, and Systematics* 36:319–344.
- UNITT, P. 2004. *San Diego County Bird Atlas*. Ibis Publishing, Vista, CA.
- VOS, C. C., J. VERBOOM, P. F. M. OPDAM, AND C. J. F. TER BRAAK. 2001. Toward ecologically scaled landscape indices. *American Naturalist* 158:24–41.
- WEBB, J. K., AND R. SHINE. 1997. A field study of spatial ecology and movements of a threatened snake species, *Hoplocephalus bungaroides*. *Biological Conservation* 82:203–217.
- WEINS, J. A., T. O. CRIST, K. A. WITH, AND B. T. MILNE. 1995. Fractal patterns of insect movement in microlandscape mosaics. *Ecology* 76:663–666.
- WHITE, G. C., D. R. ANDERSON, K. P. BURNHAM, AND D. L. OTIS. 1982. *Capture-Recapture and Removal Methods for Sampling Closed Populations*. Los Alamos National Laboratory, Los Alamos, NM.
- WILCOX, B. A., AND D. D. MURPHY. 1985. Conservation strategy: the effects of fragmentation on extinction. *American Naturalist* 125:879–887.
- WILSON, E. O. 1992. *The Diversity of Life*. Belknap Press of Harvard University Press, Cambridge, MA.
- WILSON, L. D. 1970. The Coachwhip Snake, *Masticophis flagellum* (Shaw): taxonomy and distribution. *Tulane Studies in Zoology and Botany* 16:31–99.
- WOODROFFE, R., AND J. R. GINSBERG. 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280:2126–2128.
- YAACOB, G., Y. ZIV, AND M. L. ROSENZWEIG. 2007. Habitat fragmentation may not matter to species diversity. *Proceedings of the Royal Society of Britain* 274:2409–2412.

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